

Re-analysis of a banding study to test the effects of an experimental increase in bag limits of mourning doves

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ABSTRACT *In 1966-1971, eastern US states with hunting seasons on mourning doves (*Zenaidura macroura*) participated in a study designed to estimate the effects of bag limit increases on population survival rates. More than 400 000 adult and juvenile birds were banded and released during this period, and subsequent harvest and return of bands, together with total harvest estimates from mail and telephone surveys of hunters, provided the database for analysis. The original analysis used an ANOVA framework, and resulted in inferences of no effect of bag limit increase on population parameters (Hayne 1975). We used a logistic regression analysis to infer that the bag limit increase did not cause a biologically significant increase in harvest rate and thus the experiment could not provide any insight into the relationship between harvest and annual survival rates. Harvest rate estimates of breeding populations from geographical subregions were used as covariates in a Program MARK analysis and revealed an association between annual survival and harvest rates, although this relationship is potentially confounded by a latitudinal gradient in survival rates of dove populations. We discuss methodological problems encountered in the analysis of these data, and provide recommendations for future studies of the relationship between harvest and annual survival rates of mourning dove populations.*

1 Introduction

The mourning dove is the most ubiquitous game bird in the United States, and its annual harvest during the fall hunting seasons in 39 of the 50 states exceeds by far

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all other North American game species (Reeves & McCabe, 1993). Breeding populations in the northernmost regions of its range tend to migrate south to winter, while populations in the southern US are relatively sedentary (Tomlinson, 1993). Based upon an analysis of band returns by Kiel (1959), the US is divided into three operational management regions: the Eastern Management Unit (EMU), which includes states between the Atlantic coast and the Mississippi River, the Western Management Unit (WMU), which contains states west of the Continental Divide, and the Central Management Unit (CMU), which contains the interior of the country.

During the late 1960s and early 1970s, multi-year, large-scale banding studies were done in each management unit to improve understanding of population demographics by providing the data for estimation of survival rates, harvest rates, and distribution patterns. The most ambitious of these studies was done in the EMU. Between 1966 and 1972, a cooperative study by the US Fish and Wildlife Service and the Southeastern Association of Game and Fish Commissioners examined the response of population and harvest parameters to an experimental increase in bag limit. There are 27 states in the EMU, 16 of which allowed hunting of doves (Table 1), and the normal daily bag limit was 12. After three hunting seasons designated as controls (1966-1968), the bag limit was increased for 2 years (1969-1970) to 18 birds in all hunting states (with the exception of Pennsylvania and West Virginia), and then returned to the normal level for the final hunting season of the study (1971). Several thousand birds were banded each year during the breeding season, and band recoveries were compiled by the US Fish and Wildlife Service Bird Banding Laboratory. Mail and telephone surveys of hunters provided estimates of harvest and hunter activity during the same years. Primary interest was in the detection of measurable change in first season (direct) band recovery and annual survival rates, as well as changes in harvest effort and success (Hayne, 1975).

Analysis and publication of the results of this study were completed (Hayne, 1975) prior to the publication of Brownie *et al.* (1978), which initiated a new era of estimation and model selection techniques for band recovery data. Thus, survival estimates were based on models that are considered rudimentary by today's standards, but were state-of-the-art at the time. Brownie *et al.* (1978) models were used by Martin & Sauer (1993) to analyse these data as a part of a general

TABLE 1. Groups of states used in Hayne's analysis of the effect of bag limit increase on dove population parameters

Group	States
Gulf Coast (GC)	Florida, Louisiana, Mississippi
Mid-Atlantic (MA)	Delaware, Maryland, Pennsylvania, Rhode Island, West Virginia
Mid-central (MC)	Illinois, Kentucky, Tennessee
Northeast ¹ (NE)	Connecticut, Maine, Massachusetts, New Hampshire, New Jersey, New York, Vermont
Northwest ¹ (NW)	Indiana, Michigan, Ohio, Wisconsin
South-Atlantic (SA)	North Carolina, South Carolina, Virginia
South (SS)	Alabama, Georgia

¹Non-hunting regions.

summary of the population demography of EMU doves, but they did not attempt a synthetic re-analysis of the bag limit experiment per se.

Hayne employed an analysis of variance philosophy to test hypotheses about parameter changes, in contrast to the current emphasis on parameter estimation and model-based inference (Burnham & Anderson, 1998) which has been facilitated by the concurrent development of software that allows sophisticated modelling of band recovery and mark-recapture data sets (White & Burnham, 1999). The EMU study is arguably the largest-scale experiment ever done to investigate the effects of harvest on a game bird species. Very little research effort has been devoted to mourning dove population dynamics in the past 25 years, but there is now renewed interest in development of a more rigorous foundation for dove harvest management. This interest, together with the opportunity to employ a new generation of analysis techniques to a large and complex data set, was the motivation for this work. Specifically, our objectives are to use state-of-the-art techniques to (1) estimate effects of increased bag limits on recovery rates and survival rates, (2) estimate the relationship between harvest rate and annual survival rate, (3) contrast results from an estimation/modelling approach with a hypothesis testing approach, (4) identify statistical problems in the analysis of band recovery data that require further attention.

2 Hayne's analysis

2.1 Methods

A multivariate cluster analysis technique was used to assign states to a manageable number of groups, which would necessarily also have larger sample sizes. Banding data from birds harvested during the 1965-1971 hunting seasons were classified and organized using standard criteria (Nichols & Tomlinson, 1993). However, during the course of the study, the US Fish and Wildlife Service began issuing bands with revised inscriptions, and there was concern that there might be differential reporting rates associated with the two band types. Based on the results of a special field study conducted in 1971, Hayne multiplied raw numbers of recoveries of new band types by a factor of 1.09 before calculating survival and recovery rate estimates. Survival estimates for adults (AHY) in each state group were calculated using the time-specific model of Seber (1970). This model is equivalent to Model M_1 in the Brownie *et al.* (1978) model set. Survival estimates for juveniles (HY) were calculated using Ricker's (1958) 2-release method. This estimator uses the number of HY birds banded in one year, the number of AHY birds banded the following year, and the number of recoveries from each of these cohorts, to generate an estimate of HY survival rate for the year between the releases. This estimator assumes age- and time-specific survival and recovery rates, and is approximately unbiased, but it is not the fully efficient maximum likelihood estimator for the standard 2 age class, time-specific Model H_1 in Brownie *et al.* (1978). At the time of Hayne's analysis, the concept of rigorous comparison of several candidate models with different parameter structures had not been developed in wildlife science, and thus no model selection analysis was performed.

Inferences about the effects of increased bag limits on population parameters were derived based on an analysis of variance hypothesis testing philosophy. Twelve- and 18-bird bag limits were considered levels of a manipulated factor, and years were considered as independent replicates, which provided estimates of

experimental error. Secondary factors, such as state group, were incorporated as nested factors as appropriate in some analyses. Formal hypothesis tests were calculated with a Type I error rate of 0.10. Post-hoc power analysis was done to draw conclusions about the statistical sensitivity of the comparisons.

2.2 Results

The cluster analysis classified states into seven groups (Table 1). Five of the groups contained hunting states, and the remaining two comprised non-hunting states. Slightly more than 400 000 adults (AHY) and juveniles (HY) were banded during the 7 years of the study (more specific numbers are provided in the presentation of our analysis). Direct (first-season) recovery rates were numerically lower in experimental compared with control years for both age classes, although ANOVA results were not significant ($P > 0.10$). Hayne noted that recovery rates decreased during the experiment, and reported a significant ($P < 0.001$) negative linear trend of arcsine-transformed recovery rates for both age classes (Fig. 1). Recovery rates were higher in hunting than in non-hunting states ($P < 0.001$), and AHY rates were lower ($P < 0.001$) than HY rates (Fig. 1). Differences in rates between hunting and non-hunting groups of states were similar between experimental and control years, as evidenced by no significant interaction in ANOVAs. No estimates of precision were provided in the report. Hayne concluded that the ‘experiment had no detectable effect upon the first season recovery rates.’

No significant difference was found between annual survival rates in experimental versus control years for either age class (Fig. 2). Survival rates for both age classes were significantly ($P < 0.05$) lower in groups of hunting states, and survival of adults was greater than juveniles ($P < 0.001$). For adults, the ANOVA analysis detected significantly greater ($P < 0.05$) survival for males ($\bar{X} = 0.41$) than females ($\bar{X} = 0.35$). No detectable difference in survival rates was found among groups of hunting states. Hayne concluded that there was ‘no reliable evidence of a change in survival resulting from the greater bag limit during the experimental years’, and that survival in non-hunting states was generally higher.

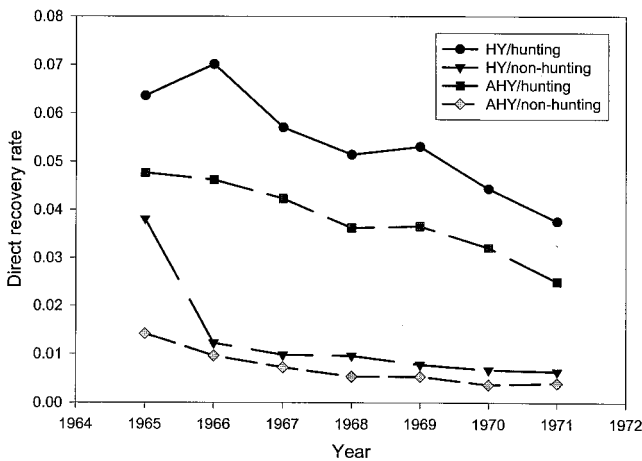


FIG. 1. Direct recovery rates of adult (AHY) and juvenile (HY) doves in hunting and non-hunting states, as reported in Hayne’s analysis.

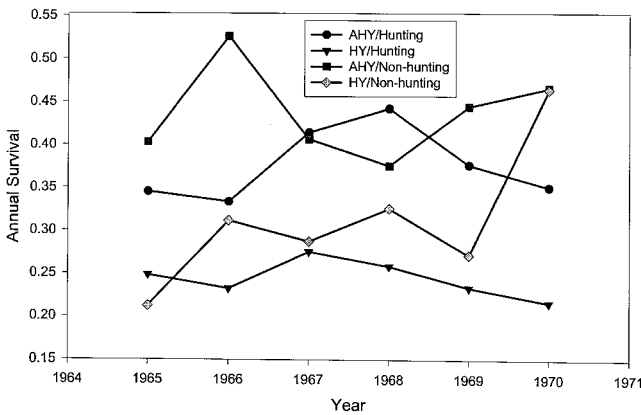


FIG. 2. Annual survival rates of adult (AHY) and juvenile (HY) doves in hunting and non-hunting states reported in Hayne's analysis.

Hayne performed post-hoc power analyses of the ANOVA hypothesis of no difference in various parameters between control and experimental years. He concluded that, with a Type I error of 0.05 and a Type II error of 0.20, the experiment could detect approximately a 20% relative change in annual survival, and a 65% relative change in direct recovery rates. Estimated changes in both parameters were less than these detectable limits.

3 Re-analysis

3.1 Methods

We did not choose to revisit the grouping of states with a revised cluster analysis because we did not want comparison of our results and Hayne's to be confounded by different state group definitions. However, we did create an eighth group (EC) by separating Pennsylvania and West Virginia from Group MA (Table 1), since the bag limit was not increased in these states during the experiment. In addition, because there were significant numbers of birds banded and recovered in 1972 and 1973 (Table 2), we included data from these years in some analyses. This decision was also consistent with our desire to produce the best possible estimates of demographic parameters for future modelling of population harvest strategies for mourning doves.

3.1.1 Effect of bag limit increase. We chose to model direct recovery rates (f') as a function of year (t), age (a), state group (region), and bag limit (B ; coded 1 in years of bag limit increase and 0 otherwise) in a logistic regression analysis. We also included models that substituted a time trend (T) for year effect. Several plausible models involving the first three variables were fit by using the Known Fate data option, the logit link function, and the Design Matrix capabilities in Program MARK. The best set of models was selected, and additional models with the same structure, but with the B variable added, were fit to examine specifically the effect of a bag limit increase on direct recovery rates. Our philosophy was first to determine directly if there was any evidence that the bag limit had increased harvest, using direct recovery rate as an index to harvest rate. Given such evidence, it then made sense to proceed with an analysis of the potential effect on survival rate.

An important difference between our analysis and Hayne's analysis was that we included non-hunting groups of states. The majority of birds from these states migrate to more southern regions during late summer and fall (Hayne & Geissler, 1977). Thus, these birds presumably would have been exposed to hunting pressure in states with increased bag limits. It is important to realize that birds that were banded during the preseason in non-hunting states are subsequently exposed to hunting during migration, albeit at a reduced level.

3.1.2 Effect of harvest on annual survival. Prior to the modelling of harvest effects, we investigated whether there was evidence of differential survival of adult male and female doves. Evidence in the literature has been inconclusive (Hayne, 1975; Martin & Sauer, 1993). Juvenile doves cannot be sexed reliably, and therefore two-age-class models require that the sexes be pooled. Thus, results of this analysis can also aid in interpretation of the two-age-class results. We first used a plausible set of models with parameter structures that involve regional and annual variation in both annual survival and recovery rate. We then selected the best subset of these models, and created additional models with the same parameter structure but with an additional parameter for sex effect. Our philosophy in this approach was that the sex effect could be evaluated more directly by using a set of models known to be parsimonious, rather than letting this *a priori* effect of interest influence the model selection process. We adopted the basic parameterization used by Seber (1970) in his treatment of band recovery models. That is, survival rate (S) is defined as the probability of annual survival between two consecutive banding periods, given that the bird is alive at the beginning of the first period, and conditional detection rate (r) is defined as the probability that a bird that dies in a given year is found and its band is reported. The latter parameter has been referred to as recovery rate (Seber, 1970) and reporting rate (White & Burnham, 1999), but we use a different term to avoid ambiguity and confusion with our previous use of recovery rate.

Although it was not a stated objective of Hayne's analysis to estimate the effect of harvest rate on survival rate, we believe the data set had the potential to provide insight into the relationship between harvest rates and annual survival rate, which is an important consideration in the management strategy for any game species. Many investigators have fit band recovery data to models that incorporate specified functional relationships between recovery rate (used as an index to harvest rate) and survival rate (Burnham *et al.*, 1984; Barker *et al.*, 1991; Rexstad, 1992). These models are generally referred to as ultrastructural models, and computations are accomplished by use of Program SURVIV (White, 1984). For example, Barker *et al.* (1991) modelled this relationship for grey ducks (*Anas superciliosa*) as

$$S = S_0(1 - bK)$$

$$K = f / ((1 - c)\lambda)$$

and S = annual survival, S_0 = annual survival with a zero harvest rate, b = a slope parameter between 0 and 1, f = probability that a bird is harvested, retrieved and its band is reported, c = crippling loss, and λ = band reporting rate. The parameter K represents kill rate, and an estimate of K clearly depends upon estimates of c and λ in addition to the estimate of f , which is generated by the band recovery modelling process. Typically, constant values for c and λ are assumed, and estimates of S_0 and b are generated and interpreted with respect to the relative support of additive (b values close to 1) versus compensatory (b values close to 0) hunting mortality hypotheses (Burnham *et al.* 1984).

We chose to take a more direct approach to learning about this relationship by using an estimate of harvest rate as a covariate in an analysis of the data using Program MARK. Harvest rate estimates were taken from a complimentary report of the study results prepared by Hayne & Geissler (1977). The emphasis of this report was on movement patterns of doves in each state, and the derivation of harvest from one state from every other state. From 1966-1971, mail and telephone surveys of hunters were the basis for estimates of total harvest in each state. These estimates were weighted by age ratios estimated from a sample of wings submitted by surveyed hunters to produce age-specific harvest estimates. Breeding population estimates in each state were derived by using numbers of birds banded and recovered, and total harvest estimates. Harvest rate for each state in each year was then obtained by dividing total harvest by population size. To obtain harvest rates for our state regions, we calculated a weighted average using population size as weights. We acknowledge that these harvest rate estimates are not strictly independent of survival rate estimates, since the population size estimates rely on the number of band recoveries in a given region.

We trimmed the data set to include only the years 1966-1971, and fit a plausible set of models without the harvest rate covariate. We then chose a best subset of these models and added harvest rate values as group covariates to generate a set of companion models for estimating harvest rate effects.

3.2 Results

3.2.1 Effect of bag limit increase. A saturated model for this analysis is $f'(a*Region*t)$, in which age (a), regional (Region), and individual year (t) all affect direct recovery rates, and the $*$ notation indicates interaction among factors. However, we chose $r(a + Region*t)$ as a global model, based on our belief that the difference between recovery rates of the two age classes should be additive and consistent across time and Regions. The fit of this model to the observed recovery rates was marginal, with an estimated $\hat{c} = 3.725$, as calculated by dividing the model deviance ($= 268.24$) by its degrees of freedom ($= 72$). This result is a clear indication that there is significant overdispersion in the data, and therefore we used the recommended quasi-likelihood adjustment (Burnham & Anderson, 1998) to the AIC, i.e. $QAIC = -[2\log(\mathcal{L}(\hat{\theta}))/\hat{c}] + 2K$. We included age as a factor in all models, as it has been well documented in the literature that recovery and harvest rates of adult doves are less than juvenile doves (Martin & Sauer, 1993; McGowan & Otis, 1996). A set of models with logical combinations of age (a), regional (Region), individual year (t), and annual trend (T) effects were fit to the data, and model $f'(a + Region*T)$ was clearly the model best supported by the data (Table 3). This model fits a different linear time trend to the logit of direct recovery rate for each Region, and forces parallelism between the age classes. The effect of bag limit increase cannot be estimated from models with independent year effects, but additional models with a bag limit effect that is the same for both age classes (B) and different for each age class (B /age specific) were fit to $f'(a + Region*T)$ and $f'(a*Region*T)$. For both sets of models, there was indication that bag limit had a statistically important and similar effect on rates for both age classes. Although the QAIC value for model $f'(a + Region*T, B)$ was only slightly smaller than $f'(a + Region*T)$, the decrease in deviance was 9 units. (The importance of this decrease is diluted by the use of QAIC.)

Parameter estimates generated by model $f'(a + Region*T, B)$ confirm the

TABLE 3. Program MARK summary of logistic regression modelling of the effects of bag limit increase on direct recovery rates = f' .

Model	Delta QAIC _c	Model weight	R^1	Deviance
$f'(a + \text{Region} * T, B)$	0.00	0.450	18	337.728
$f'(a + \text{Region} * T)$	0.38	0.372	17	346.609
$f'(a + \text{Region} * T, B/\text{age specific})$	1.87	0.176	19	337.245
$f'(a + \text{Region} + t)$	19.12	0.000	17	416.406
$f'(a * \text{Region} * T, B)$	20.32	0.000	33	301.666
$f'(a * \text{Region} * T)$	20.70	0.000	32	310.537
$f'(a * \text{Region} * T, B/\text{Age Specific})$	22.28	0.000	34	301.510
$f'(a + \text{Region} + T)$	24.36	0.000	10	488.083
$f'(a + \text{Region} * t)$	91.36	0.000	73	268.236
$f'(a + \text{Region})$	240.64	0.000	9	1301.155
$f'(a * \text{Region})$	252.89	0.000	16	1294.633
$f'(a * t)$	1146.60	0.000	18	4608.862
$f'(a + t)$	1168.70	0.000	10	4751.078

¹Number of estimable model parameters

expected decrease in recovery rate for the AHY (Fig. 3) and HY (Fig. 4) age classes. Estimates of trend intercept and slope parameters also provide insight into the $\text{Region} * T$ interaction. The non-hunting Regions (NE and NW) had smaller intercepts and Region SA behaved differently from the other hunting Regions. The estimated regression coefficient = 0.0542 for B suggests that recovery rates increased in years of increase bag limit (Table 4). However, the confidence interval for this parameter contained 0, due to the inflated standard errors resulting from the \hat{c} adjustment for overdispersion. In any case, the estimated average increase of 0.0014 in adult direct recovery rates and 0.0018 in juvenile recovery rates due to the bag limit increase was biologically unimportant. We did not believe such an increase could have an impact on annual survival rates, and thus we did not pursue further modelling on the demographic effects of the experimental bag limit increase.

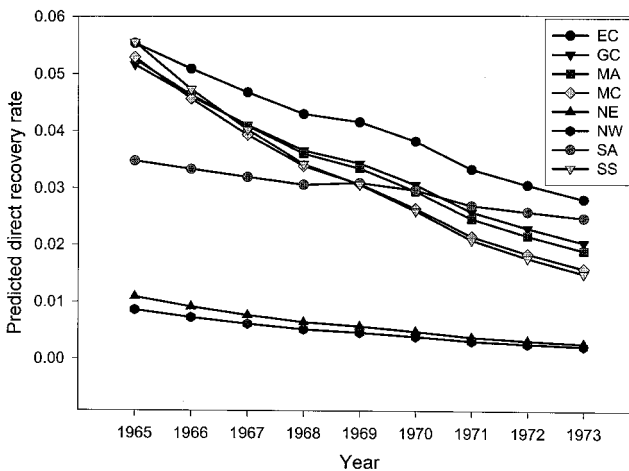


FIG. 3. Predicted regional adult recovery rates from Model $f'(a + \text{Region} * T, B)$.

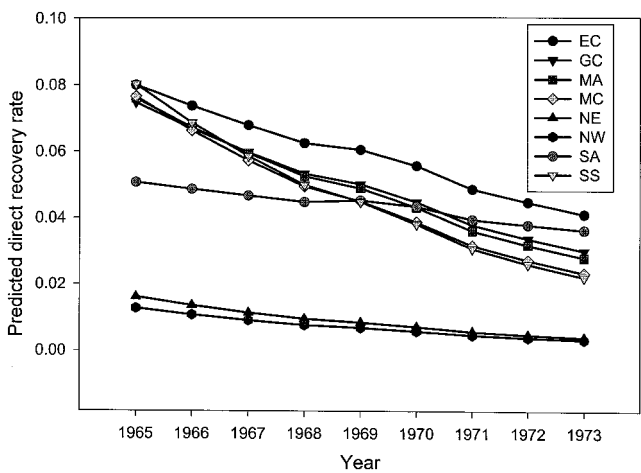


FIG. 4. Predicted regional juvenile recovery rates from Model $f'(a + \text{Region} \cdot T; B)$.

TABLE 4. Estimates of logistic regression parameters from $f'\{a + \text{Region} \cdot T, B\}$

Parameter	Estimate	Std. err.	95% Confidence interval ¹	
			Lower	Upper
Age	-0.3943	0.0370	-0.4669	-0.3217
EC intercept	-2.3533	0.2616	-2.8661	-1.8405
GC intercept	-2.3964	0.0845	-2.5620	-2.2307
MA intercept	-2.3667	0.1986	-2.7559	-1.9774
MC intercept	-2.3343	0.0887	-2.5081	-2.1605
NE intercept	-3.9342	0.3612	-4.6421	-3.2262
NW intercept	-4.1813	0.2872	-4.7441	-3.6184
SA intercept	-2.8859	0.0866	-3.0556	-2.7163
SS intercept	-2.2698	0.0788	-2.4243	-2.1153
EC slope	-0.0892	0.0369	-0.1617	-0.0167
GC slope	-0.1205	0.0162	-0.1524	-0.0887
MA slope	-0.1319	0.0374	-0.2054	-0.0585
MC slope	-0.1561	0.0190	-0.1933	-0.1188
NE slope	-0.1778	0.0629	-0.3011	-0.0545
NW slope	-0.1713	0.0517	-0.2726	-0.0699
SA slope	-0.0443	0.0149	-0.0730	-0.0150
SS slope	-0.1696	0.0181	-0.2051	-0.1341
Bag limit	0.0542	0.0350	-0.0144	0.1229

¹ Estimate $\pm 1.96 \cdot \text{Std. Err.}$

3.2.2 Effect of sex on adult survival. The fit of our global model $\{S(\text{Region} \cdot t), r(\text{Region} \cdot t)\}$ was evaluated using the Pearson chi-square algorithm in Program ESTIMATE (Brownie *et al.* 1978) by fitting the time-specific model to each Region/sex data set, and pooling the results. Only four state regions (GC, MC, SA, SS) had adequate data to perform the test. This analysis resulted in an estimated $\hat{c} = \chi^2/\text{df} = 1.732$, which was used to adjust AIC values to QAIC.

The best conditional detection rate structure was a trend model for each Region ($\text{Region} \cdot T$), which is consistent with the preceding direct recovery rate analysis. Four models of survival rate, $S(t)$, $S(\text{Region} + t)$, $S(\text{Region})$, and $S(\cdot)$, all had

TABLE 5. Program MARK summary of models used to assess the effect of sex on survival of adult mourning doves

Model	Delta QAIC	Model Weight	R^1	Deviance
$\{S(\text{sex} + t), r(\text{Region} * T)\}$	0.00	0.260	26	764.463
$\{S(\text{sex} + \text{Region} + t), r(\text{Region} * T)\}$	0.16	0.240	33	740.604
$\{S(t), r(\text{Region} * T)\}$	0.62	0.191	25	768.977
$\{S(\text{Region} + t), r(\text{Region} * T)\}$	1.48	0.124	32	746.323
$\{S(\text{sex}), r(\text{Region} * T)\}$	2.81	0.064	18	796.880
$\{S(\text{sex} + \text{Region}), r(\text{Region} * T)\}$	3.30	0.050	25	773.589
$\{S(.), r(\text{Region} * T)\}$	3.51	0.045	17	801.543
$\{S(\text{Region}), r(\text{Region} * T)\}$	4.65	0.025	24	779.361
$\{S(\text{Region} + t), r(\text{Region} * t)\}$	37.67	0.000	87	619.002
$\{S(\text{Region}), r(\text{Region} * t)\}$	39.77	0.000	80	646.768
$\{S(\text{Region} * t), r(\text{Region} * T)\}$	59.56	0.000	88	653.259
$\{S(\text{Region} * t), r(\text{Region} + t)\}$	89.03	0.000	88	704.046
$\{S(\text{Region} * t), r(\text{Region} * t)\}$	101.75	0.000	136	560.299
$\{S(\text{Region} * t), r(t)\}$	136.21	0.000	81	809.480
$\{S(t), r(t)\}$	867.23	0.000	17	2289.728
$\{S(\text{Region}), r(t)\}$	2446.50	0.000	17	5010.975
$\{S(\text{Region}), r(\text{Region} + t)\}$	2817.70	0.000	22	5633.171

¹ Number of estimable model parameters

roughly equal QAIC values when combined with $r(\text{Region} * T)$. An additive sex-effect parameter was added to each of these to create four new models. In each case, the sex effect model had a lower QAIC value than its counterpart, and the 95% confidence interval for the logit coefficient for the sex effect did not include zero (Table 5). Thus, the weight of evidence supports an inference that adult survival rates differ by sex. Using the model $\{S(.), r(\text{Region} * T)\}$, the estimated average male adult survival is 0.4108 ($\hat{SE} = 0.0088$), and the estimate for females is 0.3815 ($\hat{SE} = 0.0108$). This difference may represent a source of some lack of fit to two age class models in which sexes are pooled, and it could be used in subsequent development of demographic models of this population.

3.2.3 Effect of harvest on annual survival. The fit of our global model $\{S(a * \text{Region} * t), r(a * \text{Region} * t)\}$, where a represents an age effect, was evaluated using the Pearson chi-square algorithm in Program BROWNIE (Brownie *et al.*, 1978) by fitting the time-specific model to each Region/age data set, and pooling the results. This analysis resulted in an estimated $\hat{c} = \chi^2/\text{df} = 1.33$, which was used to adjust AIC values to QAIC.

We specified a set of plausible structures for conditional detection rate, and paired these with a restricted set of survival rate structures (Table 6). This initial phase of the analysis led to a decision to select the $r(a + \text{Region} * t)$ structure for conditional detection rate. We then added several additional models generated by a supplemental set of structures for survival rate. The three models $\{S(a * \text{Region}), r(a + \text{Region} * t)\}$, $\{S(a * \text{Region} + t), r(a + \text{Region} * t)\}$ and $\{S(a + \text{Region}), r(a + \text{Region} * t)\}$, were the most plausible set of models for the data set. However, comparison of the deviances from the first two of these models revealed that the model with an additive time effect for survival rate did not represent an improvement over its counterpart no-time-effect model, because the difference in deviance was almost exactly equal

TABLE 6. Groups of states used in Hayne’s analysis of the effect of bag limit increase on dove population parameters

Model	Delta QAIC	Model weight	R^1	Deviance
$\{S(a*Region) \ r(a + Region*t)\}$	0.00	0.909	65	368.224
$\{S(a + Region + \bar{h})\ r(a + Region*t)\}$	5.07	0.072	59	390.945
$\{S(a*Region + t) \ r(a + Region*t)\}$	7.94	0.017	70	365.486
$\{S(a + Region) \ r(a + Region*t)\}$	13.21	0.001	58	404.429
$\{S(a + Region + t) \ r(a + Region*t)\}$	20.86	0.000	63	401.291
$\{S(a + Region*t) \ r(a + Region + t)\}$	34.57	0.000	63	419.547
$\{S(a + Region*t) \ r(a + Region*T)\}$	38.87	0.000	66	417.271
$\{S(a + Region*t) \ r(a + Region*t)\}$	44.22	0.000	98	339.212
$\{S(a + Region) \ r(a + Region*T)\}$	47.46	0.000	26	535.155
$\{S(a + \bar{h}) \ r(a + Region*t)\}$	63.63	0.000	52	487.469
$\{S(a + Region + t) \ r(a + Region*T)\}$	64.08	0.000	24	562.592
$\{S(a*\bar{h}) \ r(a + Region*t)\}$	67.16	0.000	53	489.515
$\{S(a + Region + t) \ r(a + Region + t)\}$	72.30	0.000	28	562.882
$\{S(a) \ r(a + Region*t)\}$	77.92	0.000	51	509.149
$\{S(a*Region*t) \ r(a + Region*t)\}$	80.73	0.000	145	262.658
$\{S(a + t) \ r(a + Region*t)\}$	83.99	0.000	56	503.917
$\{S(a + Region*t) \ r(a + t)\}$	124.43	0.000	56	557.709
$\{S(a*Region*t), \ r(a*Region*t)\}$	127.22	0.000	192	199.554
$\{S(a + Region + t) \ r(a + t)\}$	1585.4	0.000	21	2594.666

¹Number of estimable model parameters

to twice the difference in the number of parameters (Table 6). Thus, we inferred that there was not strong evidence for annual variation in survival rates in the data set. This conclusion rendered further modelling of the effects of annual harvest rate on survival rate a moot point, since there is not significant variation to model.

Given the assumption of constant survival rate, we averaged 1966-1971 harvest rates for each Region and age class (Table 7), and used this variable as a group covariate (\bar{h}). Although the model $\{S(a*Region), \ r(a + Region*t)\}$ had the minimum QAIC value, it cannot be used to investigate the effect of harvest rate on survival, because the covariate \bar{h} is completely confounded with the $a*Region$ effect. Examination of the age and Region specific survival rates revealed that the source of the interaction was Region NE. That is, for all other Regions, there was a relatively constant difference between AHY and HY survival (AHY > HY), but in Region NE, HY survival was actually greater then AHY survival. We do not

TABLE 7. Average adult (AHY) and juvenile (HY) harvest rates used as covariates in analysis of effect of harvest on annual survival rate

Region	AHY	HY
EC	0.083	0.134
GC	0.088	0.150
MA	0.092	0.118
MC	0.082	0.133
NE	0.016	0.031
NW	0.020	0.035
SA	0.085	0.116
SS	0.142	0.202

TABLE 8. Estimates, standard errors and confidence intervals for survival rate logit function parameters in the model $\{S(\text{Region} + a + \bar{h}), r(a + \text{Region} * t)\}$

Parameter	Beta	Std.Err. ¹	95% Confidence interval	
			Lower	Upper
Age	0.1460	0.1300	-0.1087	0.4007
\bar{h}	-7.7391	2.4400	-12.5216	-2.9566
EC Region	-0.0513	0.3830	-0.6993	0.8020
GC Region	0.1078	0.3613	-0.6004	0.8160
MA Region	-0.0350	0.3284	-0.6787	0.6087
MC Region	0.0160	0.3302	-0.6313	0.6633
NE Region	0.7845	0.2625	0.2699	1.2991
Region	0.0773	0.1908	-0.2965	0.4512
SA Region	0.0623	0.3054	-0.5363	0.6608
SS Region	0.7075	0.4860	-0.2450	1.6601

¹Standard errors and confidence intervals have been adjusted by $\hat{e} = 1.334$.

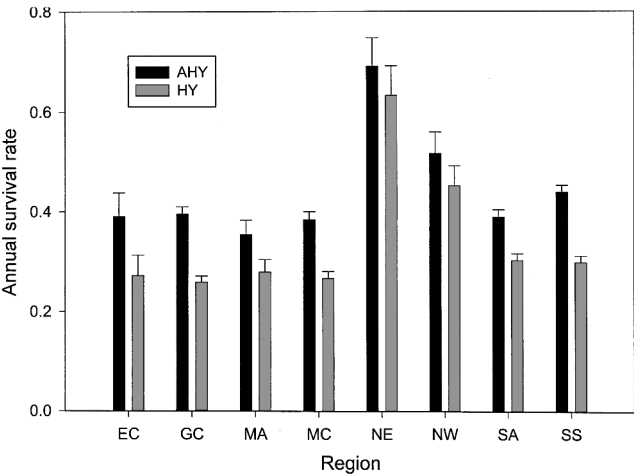


FIG. 5. Annual survival rate estimates and standard error bars for adult (AHY) and juvenile (HY) mourning doves in each region, produced from Model $\{S(a + \text{Region} + \bar{h}), r(a + \text{Region} * t)\}$.

have a plausible biological explanation for this outcome, and we chose to use model $\{S(a + \text{Region}), r(a + \text{Region} * t)\}$, which forces AHY survival to be greater than HY survival in Region NE, as a reference model for the covariate \bar{h} . This new model $\{S(a + \text{Region} + \bar{h}), r(a + \text{Region} * t)\}$ had the minimum QAIC value among all additive effect models (Table 6). The confidence interval for the \bar{h} coefficient in the logit equation did not include zero (Table 8).

Survival estimates from model $\{S(a + \text{Region} + \bar{h}), r(a + \text{Region} * t)\}$ indicate large differences among state regions and age classes (Fig. 5). Adult survival averages 10% greater than juvenile survival in all regions. Particularly noteworthy are the higher survival rates in the NE and NW non-hunting regions.

4 Discussion

Our re-analysis provided new insights into the results of the experimental bag limit increase study. Although Hayne did consider direct recovery rate as a parameter

of interest, it was only one of a suite of variables used to assess the potential effects of the experiment. Our reasoning was that it should first be determined if the increase in bag limit had affected harvest rate, before estimating any consequential effects on survival rates. We used direct recovery rate as an index to harvest rate, and we did find some evidence that the increased bag limit resulted in a small increase in harvest rate. Hayne could not find such an increase and we surmise that several attributes of our analysis resulted in a more efficient analysis of the data. We were able to eliminate the potentially confounding effect of a decreasing trend in recovery rates during the years of the study by modelling this trend independent of the effect of bag limit. Our analysis could also accommodate the inclusion of non-hunting regions into the analysis, since these populations were also subjected to harvest in states with increased bag limit during the course of migration from their northern breeding areas. Finally, our analysis was sufficiently flexible to model data from West Virginia and Pennsylvania, which did not participate in the experiment, but nevertheless are hunting states.

Although our results provided some statistical support for an effect on harvest rates, the estimated increases were biologically negligible, and in this strict sense our results are in agreement with Hayne's. However, we are forced to the unfortunate conclusion that the regulatory change in bag limit failed to produce the desired experiment, in the sense that there was no basis for inference on the effects of harvest regulation change on survival rates. The study, however, is a practical illustration of the phenomenon of partial controllability that arises in attempts to learn about population dynamics of game species in an adaptive management framework (Johnson *et al.*, 1997).

Although it was not a stated objective of either the study or Hayne's analysis to make more general inferences about the relationship between harvest rate and annual survival rate, we chose to pursue this objective, given the availability of a data set with considerable spatial and temporal extent. We were aided by the availability of additional sources of harvest data that allowed us to model the survival-harvest relationship in a manner different from an ultrastructural approach that has been often used with band recovery data. Using the flexible modelling capabilities of Program MARK, and the philosophy of parsimonious model building as a framework for statistical inference, we drew important conclusions about population biology of EMU mourning doves at the time of the study. Adult males have consistently higher survival rates than adult females and, more importantly, there is considerable variation among geographic regions in survival of both adults and juveniles. Some of this variation can be ascribed to corresponding variation in harvest rates, i.e. breeding populations from regions with higher harvest rates tended to exhibit reduced annual survival. This latter result was mainly due to the high survival of populations from the northern non-hunting regions. This result could also be explained by a hypothesis that suggested populations from more northern regions of a species range have intrinsically higher survival rates due to ultimate environmental and habitat factors. Because there are no non-hunting states in southern regions, and no hunting states in the northernmost regions of the EMU, this confounding cannot be unravelled. New attempts at true harvest experiments may be justified, given the suggestion of a negative relationship in our analysis, and evidence of recent breeding population declines (Dolton & Smith, 2000). At the least, our estimates provide a solid foundation for comparison with results from current or future population demographic studies, and a starting point

for parameterization of population models that can be used to simulate effects of various harvest management regimes on population status.

During the course of our analysis, we encountered several problematic methodological issues that deserve attention. A fundamental step in the modelling paradigm we employed is the assessment of the goodness of fit of the specified global model for the data (Burnham & Anderson, 1998). Typically, this model is one in which the parameters are time-specific, and also vary with age, geographical region, treatment category, etc. In the analysis of live resight/recapture data, the model is derived from the standard Cormack-Jolly-Seber model structure, and a goodness of fit test suggested by Burnham *et al.* (1987) is employed. This test is available as an option in Program MARK, but its operating characteristics have been questioned when sample sizes are small, and cells with small expectations must be pooled. As an alternative, Program MARK provides an option for conducting a parametric bootstrap test when no individual covariates are contained in the model. Although the bootstrap procedure for dead recovery data is available in Program MARK, its operating characteristics are largely unknown. Furthermore, implementation of the bootstrap for our dataset would have required a prohibitive amount of computational resources. As a third alternative, the deviance can be treated as a goodness of fit statistic and compared with a chi-square statistic with degrees of freedom equal to the number of unique encounter histories minus the number of estimated parameters (Burnham & Anderson, 1998). However, the asymptotic distribution of this statistic is not chi-square if the number of unique encounter histories tends to increase with overall sample size and the expected values of encounter histories remains small (Hosmer & Lemeshow, 1989). Thus, assessment of goodness of fit for models based on marked animal data is plagued with the same problems often encountered in the use of logistic regression models.

Based upon the above considerations, we chose to revert to the standard Pearson chi-square goodness of fit statistic for time-specific dead recovery models presented in Brownie *et al.* (1978), because of the very large sample sizes of released cohorts. This test as programmed in BROWNIE contains a pooling algorithm for small expected values, and such pooling was necessary even for our large samples because of the long duration of the study relative to the average life-span of a dove. We used the results from this test to compute a \hat{c} value that was then used to generate QAIC values for model selection. These \hat{c} values differed from the values generated by using the deviance statistic in Program MARK, which does not involve a pooling algorithm. For example, the Pearson-generated \hat{c} values for the global models in the adult sex effect and survival-harvest rate analyses were 1.723 and 1.330, and the corresponding deviance values from Program MARK were 1.837 and 1.706. Because of the critical importance of this statistic to the entire model selection procedure and the subsequent estimates of parameter precision, we suggest that additional research into the operating characteristics of alternative goodness of fit procedures is necessary.

A second methodological problem we faced was the choice of a model structure for the relationship between annual survival and harvest rate. Models with structures such as $S = S_0(1 - bK)$ or $S = S_0(1 - K)^b$ have some intuitive appeal, but they are nonlinear functions, and thus do not fit within the linear modelling framework of Program MARK. In typical band recovery applications, there is also inherent statistical correlation between S and K , because K is, in turn, a function of the recovery or detection rate parameter in the model. In our situation, we were fortunate to have an independent source of information about harvest rate, and

thus it seemed logical simply to include harvest rate as another linear component in the modelling of logit (S). Although it could be argued that such a simple relationship between survival and harvest rate is flawed because survival is not constrained to the interval $\{0,1\}$, we believe the relationship is plausible within the range of harvest rates encountered in real world applications, i.e. between 0 and 0.30. Our model and the nonlinear models assume a continuous relationship between survival and harvest—there is no structure to accommodate a threshold below which harvest mortality is completely compensatory. In this regard, perhaps the models are biologically suspect. Further development of realistic functional relationships, and the software capability to easily construct the models and do the associated numerical analysis, is an important research need.

We suggest that the two different parameterizations used in band recovery models require some clarification. In his original development, Seber (1970) did not formulate his model specifically for game birds, and thus not all recoveries were derived from banded animals killed during the hunting season. Therefore, recovery rate as he defined it was affected by natural as well as harvest mortality rate. Brownie *et al.* (1978) also used the term recovery rate, and defined it (f) as the probability that a bird alive at the beginning of the hunting season is shot, and its band is reported, i.e. $f = (1 - S)r$. Thus, as White & Burnham (1999) point out, this parameter depends on survival as well as reporting rate (λ = the probability that the band from a harvested bird is reported) processes. This parameterization has been adopted for use in the management of game birds, because the vast majority of bands do accrue during the hunting season, and because Brownie's recovery rate is a logical index to harvest rate. However, this model structure does not lend itself to modelling of survival with covariates, as it becomes unclear how to model the survival portion of the f parameter with the same relationship as is used in the S parameter. This is the reason we chose to use Seber's model, i.e. r is defined conditionally on the animal dying, and thus is independent of the survival process. It should be clarified, however, that $\lambda \neq r$. Comparison of the two models reveals that, when only recoveries from hunters are used in the analysis, $\lambda r = 1 + \theta/h$, where h = harvest rate and θ = non-hunting mortality rate. Thus, the relative difference in these parameters depends on the ratio of annual non-hunting versus hunting mortality. Another important difference is that Seber's formulation constrains estimates of survival to $\{0,1\}$, while the Brownie *et al.* model allows estimates > 1 . Both parameterizations have advantages (White & Burnham, 1999), but users should be cognizant of the different interpretations required.

We note that this study provides valuable guidance for the design of future harvest experiments that might be conducted on mourning dove populations. First, it illustrates the weaknesses and risks inherent in quasi-experiments, i.e. studies in which random allocation of treatments to experimental units is not incorporated into the design. The lack of both temporal and spatial randomization was costly, in the sense that an underlying time trend in recovery rates was an important confounding source of variation in Hayne's analysis and interpretation. Although it may be politically unrealistic to randomly assign different harvest regulations to different geographical regions, an intermediate approach could be randomly to assign to regions in similar latitudes a sequence of harvest regulations (e.g. restrictive, liberal, normal), each of which is in effect for at least 2 years, in such a manner that temporal effects are balanced out, as in cross-over designs. Secondly, the reality of the partial controllability phenomenon observed in this experiment suggests that restrictive and liberal regulations should be as extreme as possible,

e.g. doubling or halving normal bag limits. Although Hayne (1975) provided post-hoc analyses of the precision and power achieved with sample sizes between 25 000 and 100 000 birds banded per year, adequate sample sizes in future experiments would be determined by the study objectives and experimental design, and calculations should account for expected changes in reporting and harvest rates that may have occurred since the time of the original study.

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